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Particulate matter production and consumption in deep mixed layers: observations in a warm-core ring

J. K. B. BISHOP,* M. H. CONTE,* P. H. WIEBE,† M. R. ROMAN‡ and C. LANGDON*

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Abstract—Particulate matter variability is described in the context of biological and physical processes in the core waters of WCR 82B between February and late June 1982. WCR 82B formed in mid-February with a probable mixed layer depth of 50 m. A series of heat loss and convective mixing events deepened the mixed layer to >300 m by March and to 400 m by early April 1982. Periods of convective mixing and transient stratification in the deep mixed layer were indicated by chlorophyll, nutrient, and temperature data collected during the last 10 days of April. Seasonal stratification was established by early May, and the core waters of WCR 82B became strongly stratified shallower than 40 m by June.

Particulate matter samples were collected from the upper 1000 m by large volume *in situ* filtration in April and June 1982. Vertical distributions were obtained for particulate dry weight, organic carbon, calcium, biogenic silicon, and phosphorus as well as abundances of >1 mm size fecal matter and fecal pellets.

The data show that particle production exceeded particle consumption by zooplankton in the euphotic zone from February to April. However, the particle concentration remained nearly constant in the euphotic zone, but increased between 50 and 400 m during this period. These observations suggest that mixed layer convection in March and April removed a significant fraction of particles from the euphotic zone into the deep thermostad. Analysis of the data shows that 67% of primary produced carbon was mixed into the thermostad during this time. Such conditions were favorable for the growth of herbivorous zooplankton which were dispersed several hundred meters below the surface. Comparisons of the standing stock of particles present in the upper 400 m in late April with supply rates of material due to down mixing suggest that the particle populations in this zone turn over on time scales of 10 days.

After onset of seasonal stratification in early May, the down-mixed supply of newly produced carbon to deep thermostad waters was eliminated. Because the rates of euphotic zone particle production and loss were no longer balanced, a bloom of phytoplankton peaking in mid-May may have occurred. Observations showed that particles were removed from the thermostad between April and June, and calculations suggest that this loss (by zooplankton consumption) may have occurred in as short a time as one week following seasonal stratification. Following the removal of utilizable particulate matter, zooplankton shoaled to become concentrated in the upper 50 m by June. The continued high rate of primary production and the strongly increased zooplankton biomass in the upper 50 m in June resulted in enhanced production of fecal material in the upper 40 m. The high rates of zooplankton grazing in June resulted in the removal of most aggregate material by 110 m.

These observations demonstrate that the coupling of physical, biological and chemical processes in the upper ocean occurs on time scales as short as 10 days. They also show that particulate matter is a sensitive indicator of the balance between production and removal processes in the upper 1000 m. Our data suggest that (1) zooplankton consumption as opposed to dark respiration is the dominant loss mechanism for phytoplankton carbon mixed below the euphotic zone into deep mixed layers, and (2) the imbalance between production and removal processes in the euphotic zone at the time of stratification caused by the cessation of mixing to depths below the euphotic zone leads to the development of the spring phytoplankton bloom.

* Lamont-Doherty Geological Observatory of Columbia University, Palisades, NY 10964, U.S.A.
† Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A.
‡ Horn Point Laboratories, University of Maryland, P.O. Box 775, Cambridge, MD 21613, U.S.A.

INTRODUCTION

PARTICULATE matter cycling has a major impact on the distributions of many dissolved chemical species in the ocean water column. In the open ocean, most particulate matter in the upper kilometer is biogenic, and biological processes are dominant in controlling particle distributions (see e.g. BISHOP *et al.*, 1977; KNAUER *et al.*, 1979; LEE and CRONIN, 1982; BETZER *et al.*, 1984). The dominant source of oceanic particulate matter is primary production; the primary mechanism of particle repackaging and consumption is zooplankton feeding and metabolism; and the dominant mode of vertical transport of particles is the settling of fecal material at 100 s of meters per day. Thus the fates of many chemical species in the water column are closely tied to the carbon cycle and food web dynamics.

The physical environment (light, mixing, nutrients, and temperature) is of major importance in determining the production of particulate organic matter in the ocean. SVERDRUP (1953) wrote,

> "In order that the vernal blooming of phytoplankton shall begin it is necessary that in the surface layer the production of organic matter by photosynthesis exceeds the destruction by respiration. The destruction of organic matter by respiration goes on continuously wherever there are plants or animals, but photosynthesis can take place only in the presence of light, carbon dioxide, and nutrient salt such as nitrates, phosphates and other minor constituents."

This statement underlines the fundamental requirements that phytoplankton have for both light and nutrients in order for photosynthesis to take place. Sverdrup went on to develop the concept of critical depth. If the mixed layer extends below this depth (even in the presence of high nutrient levels), then phytoplankton do not receive enough light for growth to overcome losses due to respiration. His paper and more recent contributions (e.g. STEELE and MENZEL, 1962; PINGREE *et al.*, 1976; YENTSCH and PHINNEY, 1985) have shown how temporal variability in the depth of the mixed layer relative to the critical depth determines the timing of the spring phytoplankton bloom in temperate and subpolar latitudes. SVERDRUP (1953) also discussed how the feeding activities of zooplankton could control primary production even when optimum physical conditions for photosynthesis were present. Therefore both the physical environment of the euphotic zone and the activities of zooplankton have been identified as important to the particle cycle.

In spite of the major impact that biological and physical processes have on the distributions of particulate matter in the ocean, few studies of particulate matter geochemistry have been carried out in the context of these processes. BISHOP *et al.* (1977, 1978, 1980) related the chemistry, distributions, biology and vertical flux of particles to the physical and hydrographic structure of the euphotic zone. Links between the hydrography and physical structure of the euphotic zone and vertical particle flux at great depths have been recently described by DEUSER (1986). Biologically oriented studies of particulate matter distributions in the context of water column structure (e.g. MENZEL and RYTHER, 1960, 1961; STEELE and MENZEL, 1962; MENZEL and RYTHER, 1970) have been restricted to the determination of phytoplankton biomass indicators such as chlorophyll or particulate organic carbon. To our knowledge, no published studies of particulate matter geochemistry have included assessment of the distributions and

activities of zooplankton. All of these studies are complicated by the fact that observations were made at a single geographic point and the influence of horizontal advective processes on observed vertical distributions could not be quantified.

An excellent opportunity to further the understanding of the particle cycle in terms of physical and biological processes was the Warm-Core Rings Experiment (WCRE). This experiment studied several warm-core rings (WCR's) of the Gulf Stream in 1981 and 1982. Warm-core ring 82B was one ring which was studied at several stages over its lifetime (Fig. 1). WCRE results have shown that the core waters of WCR 82B—within 30 km of ring center and to depths of >400 m—remained mostly isolated from February 1982, when the ring was formed, to early July 1982 when a series of interactions with the Gulf Stream occurred (JOYCE and WIEBE, 1983; OLSON *et al.*, 1985; WIEBE *et al.*, 1985b; CONTE *et al.*, 1986).

NELSON *et al.* (1985) have described aspects of the particulate matter distributions in the context of the physical structure of WCR 82B in June 1982. Their data (with the exception of biogenic silica), however, were restricted to depths shallower than 100 m. NELSON *et al.* (1985) showed that the biomass concentration maximum at depths shallower than 40 m in the core waters of WCR 82B in June resulted from *in situ* growth processes and not from lateral exchange. These conclusions have been independently verified by more spatially extensive transmissometer/CTD studies of the distributions and variability of the particle field in WCR 82B in June (BISHOP and JOYCE, 1986).

In this paper we focus on the temporal evolution of particulate matter distributions in the core waters of WCR 82B from the time of its formation in February to June 1982. Convective mixing events deepened the mixed layer from 50 to 400 m between February and April. Particular emphasis is placed on biological and physical variability of the core waters of WCR 82B during the time period from 20 April to early May 1982. It was during this period that the core waters of WCR 82B experienced several convective events and showed the first signs of seasonal stratification. Seasonal stratification was established by June, and a 10 m mixed layer overlaid a pycnocline which extended to 40 m. The relative coherence of WCR 82B between February and June 1982 permits us to focus on some fundamental questions about particulate matter dynamics. (1) How did the particulate matter distributions and chemistry respond to the convective deepening of the mixed layer of WCR 82B from February to April? (2) Was there a benefit to the zooplankton community resulting from this convective mixing? (3) What was the response of the zooplankton to the onset of stratification? How was this reflected by the particulate matter field? (4) Do the same processes affecting particle distributions in rings operate in other areas of the ocean?

METHODS

Zooplankton

The >333 μm zooplankton distributions in WCR 82B were determined during R.V. *Oceanus* cruises 116, 118, and 121 in March, April and June 1982 (Table 1) using a 1 m^3 Multiple Opening/Closing Net and Environmental Sensing System (MOC-1; WIEBE *et al.*, 1976) and double MOC-1 (MOC-1D; WIEBE *et al.*, 1985a). Samples were collected using the MOC-1 in a single tow during *Oceanus* 116 over 100 m depth intervals from 0 to 400 m and over 150 m intervals from 400 to 1000 m. The MOC-1D was deployed

Table 1. *Summary of MOCNESS sampling in WCR 82B*

Date	MOCNESS Sta. No.*	Depth (m)	Date	MOCNESS Sta. No.†	Depth (m)
820315	MOC-1 -160	0–1000			
820422	MOC-1D-164	0–1000	820422	MOC-1/4–20	0–200
820422	MOC-1D-165	0–1000	820422	MOC-1/4–21	0–200
820430	MOC-1D-172	0–1000	820426	MOC-1/4–23	0–1000
820430	MOC-1D-173	0–1000	820502	MOC-1/4–29	0–200
820617	MOC-1D-178	0–1000	820614	MOC-1/4–35	0–200
820618	MOC-1D-179	0–1000	820620	MOC-1/4–39	0–200
820619	MOC-1D-180	0–1000	820621	MOC-1/4–40	0–200
820624	MOC-1D-186	0–1000	820626	MOC-1/4–44	0–200
820625	MOC-1D-187	0–1000	820627	MOC-1/4–45	0–200

* 333 μm mesh nets; 1 = 1 m^3 net opening; D = double MOCNESS.
† 64 μm mesh nets; 1/4 = 0.25 m^3 net opening.

exclusively starting with *Oceanus* 118 and samples were collected over 25 m intervals from 0 to 200 m and over 100 m intervals from 200 to 1000 m.

Greater than 333 μm zooplankton carbon biomass was calculated from displacement volumes (WIEBE *et al.*, 1985b) using the functional relationship of WIEBE *et al.* (1975). All tows taken in ring core waters, defined as being within 30 km of ring center, during the April and June cruises (Table 1) were averaged to yield a mean biomass profile for both time periods. To do this, means were computed over the 25 m depth intervals in the upper 200 m and over the 100 m intervals below 200 m. No attempt was made to distinguish day and night collections because differences due to vertical zooplankton migration caused relatively small perturbations of the zooplankton biomass profiles (WIEBE *et al.*, 1985b).

The biomass of >64 μm zooplankton was determined from collections with a 1/4 m MOCNESS (MOC 1/4) deployed on R.V. *Knorr* cruises 93 and 95 in April and June (ROMAN *et al.*, 1985). Samples were collected from 25 m depth intervals from 200 m to the surface. The collected samples were sieved through 333 μm mesh to isolate the zooplankton fraction between 64 and 333 μm in size. This was done so that the zooplankton smaller than 333 μm could be compared with the >333 μm zooplankton distributions determined by the MOC-1 and MOC-1D systems. Carbon biomass for the 64–333 μm zooplankton was calculated from displacement volumes using the functional relationship of ROMAN *et al.* (1985).

Zooplankton grazing

Grazing rates were estimated for the April and June cruise periods by *in situ* incubations using a dual isotopic labeling technique (ROMAN and RUBLEE, 1981) and shipboard incubations with selected copepod species (COWLES, 1979).

Particulate matter

The Large Volume *in situ* Filtration System (LVFS; BISHOP and EDMOND, 1976; BISHOP *et al.*, 1980) and Multiple Unit LVFS (MULVFS, BISHOP *et al.*, 1985) were deployed during *Oceanus* cruises 118, 121, and 125 in April, June and August 1982 and during *Knorr* cruise 98 to WCR 82H in September 1982 (Fig. 1). The LVFS was deployed during April and June 1982 and the MULVFS was deployed during June, August, and

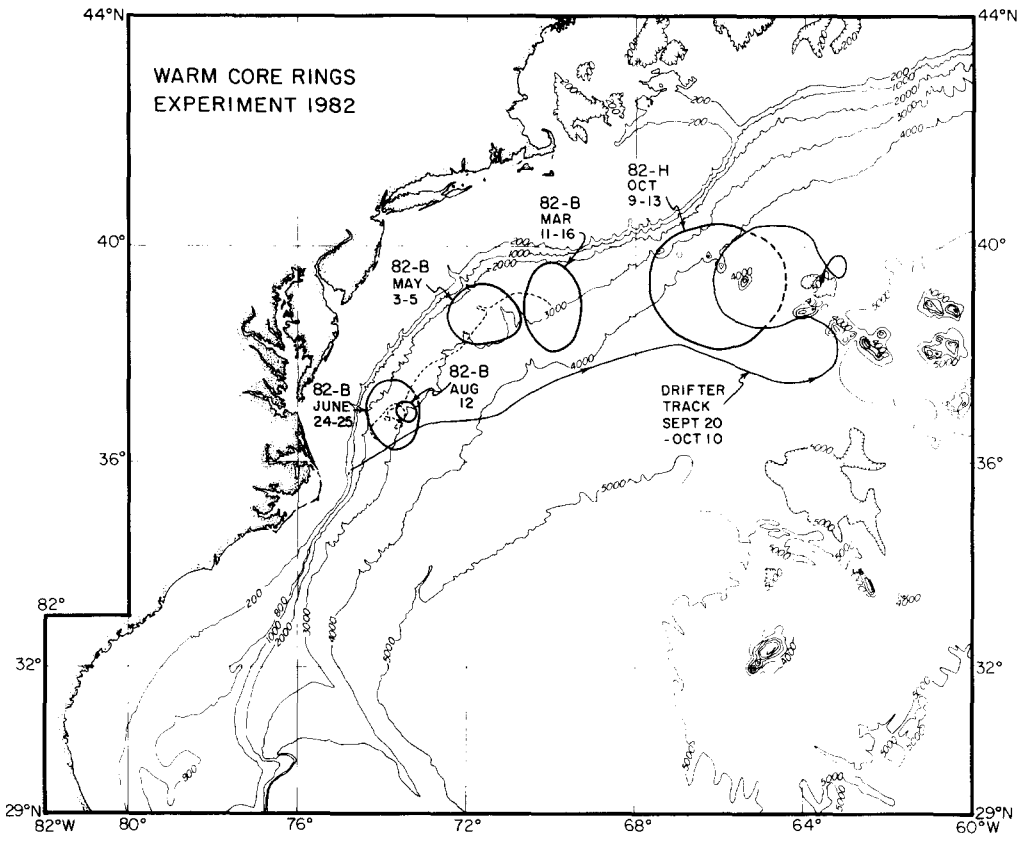

Fig. 1. Map showing the location of WCR's 82B and 82H in 1982. The track of WCR 82B is shown by dashed line. Also shown is the track of a drifter which was deployed in the center of WCR 82B in August 1982 after the ring was resorbed by the Gulf Stream in September. This drifter later became involved in the circulation of the Gulf Stream meander which formed WCR 82H.

September 1982. LVFS and MULVFS samples have been shown to be indistinguishable and therefore will be described collectively as MU(LVFS) samples (Bishop *et al.*, 1985). MULVFS data from WCR 82B in August will not be discussed in this paper since 82B had undergone a large-scale interaction with the Gulf Stream and its volume had been significantly altered.

MU(LVFS) samples consist of >53 and 1–53 μm sized particulate matter filtered from

Table 2. Summary of LVFS and MULVFS stations from ring core waters

February stations	April stations	June stations
M 820819 40–725 m	L 820422 20–200 m	M 820618 15–1000 m
M 820928 30–760 m	L 820423 110 m	L 820624 20– 600 m
M 820930 49–850 m	L 820423 200–707 m	
M 821001 10–815 m	L 820428 20–200 m	
M 821003 50–880 m	L 820501 300–600 m	
M 821007 50–815 m	M 820501 300 m	
M 821013 30–760 m		

L, Large Volume *in situ* Filtration System; M, Multiple Unit Large Volume *in situ* Filtration System.

volumes of water as large as 25 m^3. Because of ship's drift on station, each LVFS sample represents the suspended particulate matter (SPM) present at a given depth over a 1–2 km distance. Although the 64 μm net size of the MOC-1/4 is similar to the 53 μm mesh used in the MU(LVFS), the samples collected by the two systems are different due to the greatly increased flow velocity (50–100 cm s^{-1}) through the MOC-1/4 nets compared with that of the MU(LVFS) (1–2 cm s^{-1}). Experiments to determine the recovery of fragile particles, such as fecal pellets and fecal matter, as a function of flow rate indicated that the MU(LVFS) has a recovery efficiency of >90% for these particle classes but that little of this material would be preserved at flow rates used in MOC-1/4 sampling (BISHOP, 1982). On the other hand, mobile zooplankton actively avoid the MU(LVFS). For example, comparisons of copepod catch by MOC-1 and the LVFS in the euphotic zone in the Panama Basin (BISHOP *et al.*, 1986) showed that the LVFS catch was <40% of the MOC-1 catch, in spite of the fact that the LVFS used a smaller mesh size.

The two size fractions, collected by 53 μm mesh Nitex and a pair of 1 μm microquartz filters in series, were chosen such that the portion of particulate matter important to the verical flux—the >53 μm fraction (MCCAVE, 1975) would be isolated from the 1–53 μm fraction which accounts for the bulk of the suspended particulate matter. The collected material has been analysed chemically for major and minor elements (C, H, N, P, Si, Ca, Mg, K, Na and dry weight) using methodology described by BISHOP *et al.* (1977, 1980). In this paper, data for total particulate dry weight, carbon, phosphorus, calcium and silicon in the core waters of 82B will be described.

We also present data on >1 mm sized fecal matter and >1 mm long fecal pellet abundances determined in the >53 μm fraction. Counts of these classes were made from photographic contact prints of the 53 μm Nitex samples. Exposure time was adjusted to eliminate interference from the Nitex mesh but to leave the large particles adequately resolved. All samples were exposed using these optimized conditions.

RESULTS

Formation, convective overturn and stratification of WCR 82B

Before proceeding with the description of the particulate matter and zooplankton data, it is necessary to set the stage by describing aspects of the physical and biological variability of ring core waters from the time of ring formation in February to June 1982.

WCR 82B formed in mid-February 1982 with core waters derived from transitional waters of Gulf Stream and Sargasso Sea origin. At that time, surface waters were approximately 19°C and ring diameter was approximately 150 km (JOYCE and WIEBE, 1983; EVANS *et al.*, 1985). Mixed layer depth was believed to be approximately 50 m at the time of ring formation (SCHMITT and OLSON, 1985). When 82B was first sampled in mid-March, a 310 m thick, nearly isothermal layer of 17.5°C was observed. The fact that XBT temperatures showed differences of <0.1°C between the surface and 300 m indicated that active convective mixing over this interval was in progress. By mid-April, when WCRE ships visited the ring, the thermostad had cooled to approximately 15.7°C, and its depth (based on the 15°C isotherm) had increased to over 400 m.

The increase in mixed layer depths between February and mid-April was mostly due to heat loss to the atmosphere (SCHMITT and OLSON, 1985). Rather than being a continuing process, mixed layer deepening was interrupted by 11 periods of net heat gain by ring

surface waters prior to our April sampling. Such events were also accompanied by light winds. These periods of transient stratification and quiescence have a strong impact on the primary production of the water column as will be discussed below.

Heat fluxes between WCR 82B and the atmosphere were also calculated using pooled ships' observations of atmospheric conditions in the vicinity of WCR 82B from 20 April to 6 May (T. JOYCE, personnal communication). Results showed that core waters of WCR 82B experience periods of high heat loss between 22 and 24 April (JD 112 and 114) and again from 28 to 29 April (JD 118–119). Results also showed a large diurnal fluctuation of heat balance with surface waters gaining heat in the day time and loosing heat at night. It is during the two periods of strongest heat loss that convection to greatest depths was most likely to have occurred.

Evidence for active convection in the thermostad was found in 89 XBT and 16 CTD temperature profiles made from all WCRE ships within 30 km of ring center between 20 April and 5 May (Fig. 2). The depth where temperature dropped 0.1°C below sea surface temperature was calculated for each cast and was used as an indication of the depth of the mixed layer. The 0.1°C criterion is reasonable to apply to XBT data since this is near the reproducibility of these probes. It is also applicable to the more accurate CTD data, since temperature steps of this magnitude were found separating isothermal layers. Mean

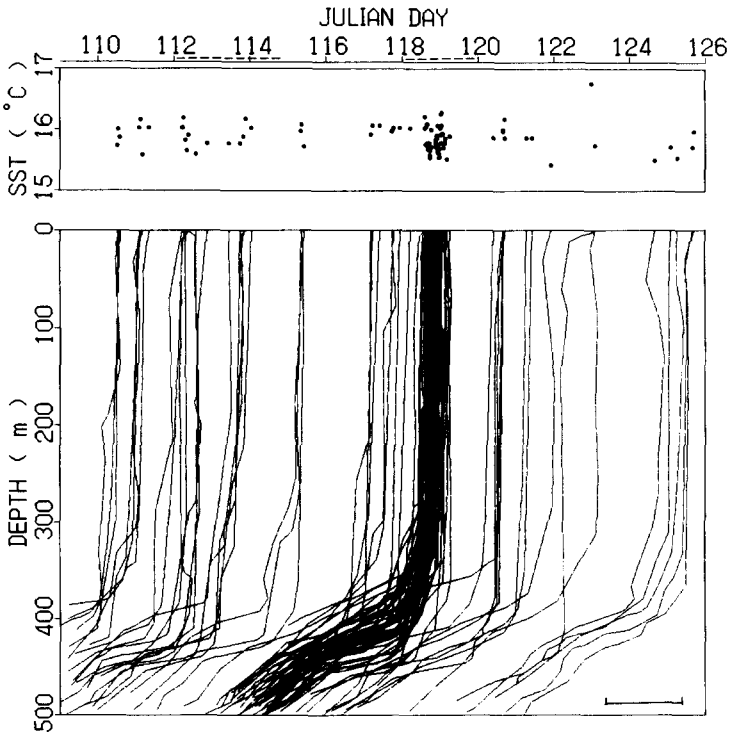

Fig. 2. Sea surface temperature (SST) and XBT profiles collected within 30 km of ring center during the period 20 April–5 May from all WCRE ships. The horizontal scale bar denotes 2°C. The profiles are offset along a time axis by making sea surface temperature equal to the time (in Julian days) of the observation. Dashed lines on the time scale denote periods of strong heat loss from the ring to the atmosphere. It is during these periods that convection to deepest depths would occur in the 400 m thermostad of WCR 82B.

mixed layer depth, as determined from the XBT and CTD data, fluctuated from 70–200 m (JD 110–113), to 280 m (JD 114), to 40–140 m (JD 116 and 117), to 190–220 m (JD 118 and 119) and to 20–150 m (JD 120–125) (Fig. 3). Deepest mean mixed layer depth was found at the end of the first heat loss event. Fewer than 25% of all observations (Fig. 4) showed mixed layer depths shallower than 50 m. Conversely, 70% of observations indicated mixed layer depths deeper than 100 m. Furthermore, 25% of observations indicated mixing to below 300 m. The depth of mixing was therefore considerably greater than the 50 m euphotic zone.

The convective overturn and stratification events indicated by the XBT/CTD data are also seen in chlorophyll profiles (Fig. 5). In mid-March, the absence of any detectable

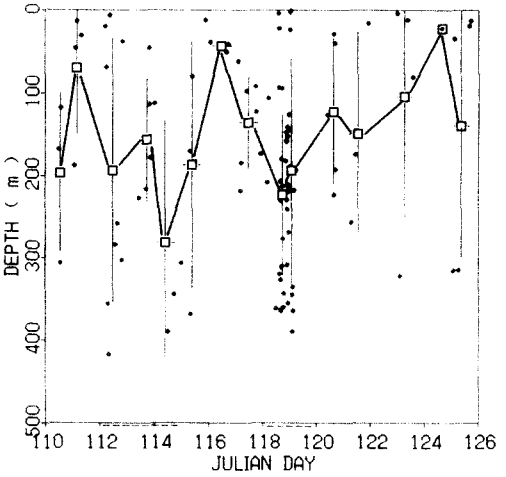

Fig. 3. Temporal variation of mixed layer depth with time. The greatest mixed layer depths were observed on days 112–114 and 118–119 when WCR 82B was experiencing large heat losses to the atmosphere.

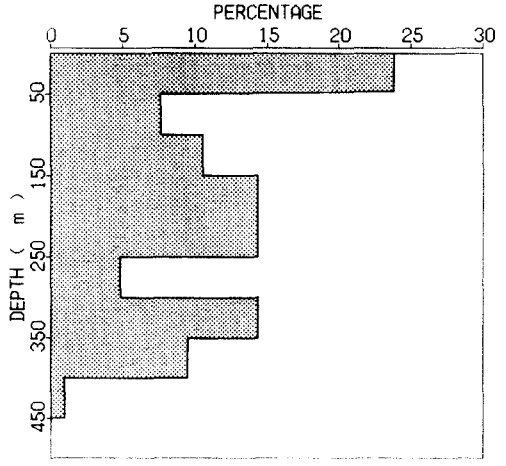

Fig. 4. Percentage frequency of mixed layer depth from 105 XBT and CTD casts within 30 km of ring center taken between 20 April and 5 May. Mixed layer depth is defined as the depth where temperature drops 0.1°C below the surface value.

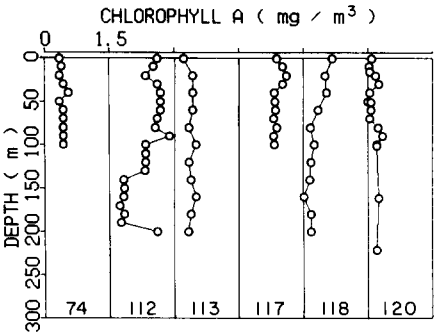

Fig. 5. Profiles of chlorophyll near ring center of WCR 82B during *Oceanus* 116 (March 1982) and 118 (April 1982). The numbers at the bottom of each plot refer to the Julian day on which each cast was made. Profiles on days 74, 113 and 120 indicate convection to great depths.

chlorophyll concentration gradient in the upper 100 m, together with undetectable temperature differences over the upper 300 m, suggests that chlorophyll may have been uniformly distributed as deep as 300 m.

Profiles of chlorophyll in April also showed evidence for convective overturn of at least the upper 200 m on 22, 23 and 30 April (JD 112, 113 and 120; Fig. 2). The only chlorophyll profile showing concentrations which decreased consistently from 0 to 200 m was collected on 28 April (JD 118). This indicated either quiescence or transient stratification of surface waters prior to this observation.

The convective mixing of chlorophyll to great depths in April also has been reported by Smith and Baker (1985) who described uniform pigment levels from the surface to 200 m near ring center. In addition, Smith and Baker (1985) reported pigment levels of 0.53, 0.61, 0.53, and 0.29 mg m^{-3} in samples collected from 190, 200, 300, and 400 m depths at another station near ring center which again indicated deep convective mixing in the thermostad.

Continuous measurements of the near-surface chlorophyll made between 22 April and 5 May 1982 from the R.V. *Knorr* within 30 km of ring center (Phinney *et al.*, 1983; Fig. 6) showed highest (up to 2.4 mg m^{-3}) chlorophyll concentrations on 22 and 23 April (JD 112–113), a second peak (again up to 2.4 mg m^{-3}) on 27 April (JD 117), and high levels (up to 2 mg m^{-3}) on 5 May (JD 125). During days between these chlorophyll peaks no observations of surface chlorophyll exceeded 1 mg m^{-3}. The temporal trend of these data is consistent with surface heat fluxes. Values of chlorophyll 0.5 mg m^{-3} were observed on all days. Such low surface chlorophyll levels were probably indicative of mixed layer convection and redistribution of chlorophyll to greater depths.

Large-scale satellite observations of the surface pigment field of ring core waters (averaged over a 33 × 33 km rectangle) indicate that two plankton blooms occurred between 18 April and 7 May (Brown *et al.*, 1985). The first bloom of chlorophyll peaked on 20 April (Julian Day 110) and was erased by 25 April (JD 115). Over this period of time, the remotely sensed pigment levels decreased by a factor of four. This loss is consistent with the stronger convective mixing (described above) of ring core waters during this time period. The onset of a second bloom was observed after 1 May (JD 121) and continued at least until 7 May, the end of the satellite coverage.

More evidence for convective mixing events was also found in 17 NO_3^- profiles of the upper 100 m reported by Fox *et al.* (1984). The lowest average nitrate for the upper

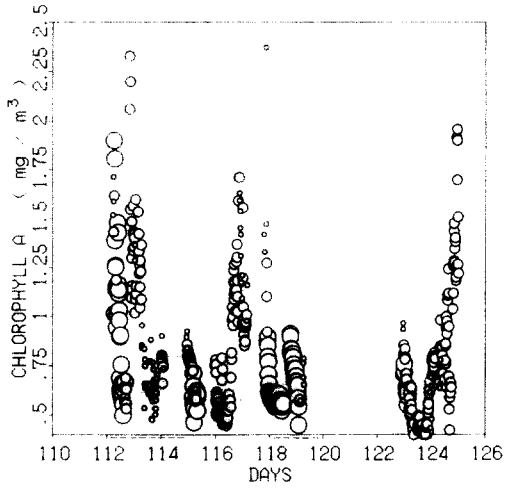

Fig. 6. Records of surface cholorphyll during 22 April–5 May (PHINNEY *et al.*, 1983). Days are in GMT time. The three sizes of symbols denote observations made 0–10 km (largest), 10–20 km, and 20–30 km (smallest) from ring center. Peak levels of chlorophyll were observed on days 112 and 113, 117 and 125. Low values are indicative of vertical convection in the mixed layer to depths below the euphotic zone. The high levels at the beginning of the cruise are consistent with a plankton bloom reported by BROWN *et al.* (1985) which peaked on day 110.

100 m (Fig. 7) of ring core waters (again defined as within 30 km of ring center) was 5.15 μmol kg^{-1} on 22 April (JD 112). Such low values were consistent with nutrient fixation by phytoplankton during the bloom reported by BROWN *et al.* (1985). Values of between 5.7 and 5.85 μmol kg^{-1} were found on 23 and 24 April (JD 113 and 114). Extensive mixing of thermostad waters is indicated on those days since these values were very close to the mean composition for thermostad waters (5.86 μmol kg^{-1}, $T > 15.1°C$)

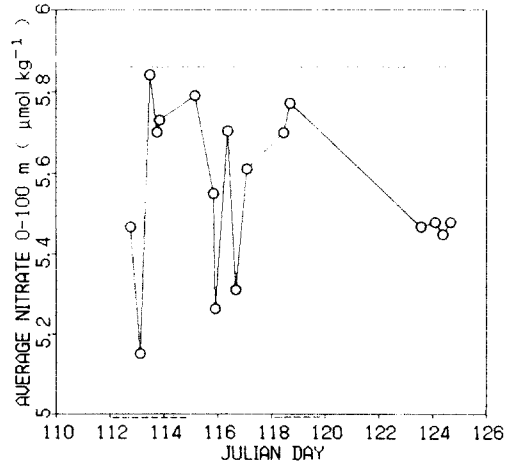

Fig. 7. Average nitrate concentration in the upper 100 m. Low values are correlated with times when surface chlorophyll values are high. The dashed line represents the mean concentration of NO_3^{-3} in thermostad waters below 100 m. Data are from FOX *et al.* (1984).

reported by Fox *et al.* (1984). Lows of 5.25 and 5.3 μmol kg^{-1} were interspersed between profiles averaging between 5.6 and 5.8 on 25 and 26 April (JD 115 and 116). These lows may have been associated either with remnant waters from the 20 April bloom which had not dispersed completely, or with quiescent waters which had lost NO_3^- due to the growth of phytoplankton. Levels between 5.7 and 5.8 μmol kg^{-1} were once again observed on 28 April (JD 118). By 3 and 4 May (JD 123 and 124), average NO_3^- dropped to 5.4–5.5 μmol kg^{-1}. The biological aspects of the near-surface nutrient variability are discussed in greater detail by McCarthy and Nevins (1986). The interpretation of cruise to cruise difference in nutrient distributions are described in detail by Fox and Kester (1986).

By June, the core waters of WCR 82B were strongly stratified with a 10 m thick mixed layer overlaying a pycnocline which extended to a depth of approximately 40 m. Nitrate was <0.1 μmol kg^{-1} in the upper 25 m (Fox and Kester, 1986) and high biomass and particulate matter concentrations were observed in the shallow pycnocline (Hitchcock *et al.*, 1985; Nelson *et al.*, 1985; Roman *et al.*, 1985; Bishop and Joyce, 1986).

Primary productivity

Primary productivity (PP) has been estimated for February and March using climatological averages of shortwave radiation (Bunker, 1976) and information on the chlorophyll content of the euphotic zone (Langdon, 1986; Table 3). Data from Cox *et al.* (1982) indicate typical February Sargasso Sea chlorophyll levels to be 0.28 mg m^{-3} (±0.14 S.D.). Our own March 1982 data showed chlorophyll averaging 0.41 mg m^{-3} in the upper 50 m (Fig. 5). From these data, we calculated PP levels of 29 ± 13 mmol C m^{-2} d^{-1} in February, 48 mmol C m^{-2} d^{-1} in March. If we use the 0.6 mg m^{-3} average of April data and the same model, we calculate a mean PP of 81 mmol C m^{-2} d^{-1}. This later value is in good agreement with the 92 mmol C m^{-2} d^{-1} mean of Hitchcock *et al.* (1985). Our calculated February level is slightly higher then Sargasso Sea values from Menzel and Ryther (1960, 1961) which ranged between 15 and 25 mmol C m^{-2} d^{-1}.

Primary productivity was determined during April and June 1982 using the ^{14}C method (Hitchcock *et al.*, 1985). April productivity ranged between 37 and 208 mmol C m^{-2} d^{-1}

Table 3. Critical depth and primary production of WCR 82B

Day	DL (h)	SW (W m^{-2})	PAR (E m^{-2} d^{-1})	I_M (μE m^{-2} s^{-1})	$\bar{I}_0$ (μE m^{-2} s^{-1})	O_2 (mmol m^{-2} d^{-1})	C	D_{CR} (m)
45	10.5	41.7	8.0	498.8	211.6	22.6	16.1	75
	10.5	115.0	22.1	1378.0	584.7	40.7	29.1	136
	10.5	173.9	33.4	2082.6	883.6	53.0	37.8	177
75	11.5	56.7	10.9	620.5	263.3	38.0	27.0	105
	11.5	160.0	30.7	1747.8	741.5	67.0	47.9	186
	11.5	236.3	45.3	2578.9	1094.2	83.8	59.9	233
120	13.5	77.8	14.9	722.6	306.6	69.0	49.3	172
	13.5	230.0	44.1	2138.7	907.4	114.0	81.4	285
	13.5	324.3	62.2	3016.5	1279.8	148.0	105.7	369

DL, day length; SW, Bunker (1976) shortwave irradiance absorbed by the sea surface (first row, overcast conditions; second row, mean cloudiness; third row, cloud free); PAR, photosynthetically active radiation; I_M, maximum PAR during light period; I_0, mean PAR; O_2, oxygen productivity; C, carbon fixation rate assuming O_2:C ratio of 1.4:1 (Langdon, 1986); D_{CR}, critical depth.

and averaged 92 mmol C m^{-2} d^{-1}. Such variability was consistent with the variability in surface chlorophyll described above. June data, in spite of a generally higher biomass concentration in the upper 50 m, averaged 58 mmol C m^{-2} d^{-1} and ranged between 21 and 81 mmol C m^{-2} d^{-1}. All but a few percent of PP occurred shallower than 50 and 25 m depths in April and June, respectively. These depths corresponded approximately to the depth where light is reduced to 3% of surface values.

For comparison, data from the Sargasso Sea near Bermuda (MENZEL and RYTHER, 1960) show that primary productivity peaks at 50–70 mmol C m^{-2} d^{-1} levels in the months of March and April, coincident with the onset of stratification, and that PP is reduced to 10–20 mmol C m^{-2} d^{-1} by June. This strong decrease did not occur in WCR 82B and is explained by enhanced nutrient fluxes into the euphotic zone through upwelling induced by the frictional decay of the ring (FRANKS *et al.*, 1986; NELSON *et al.*, 1986).

Critical depth

The comparison of critical depth and mixed layer depths gives an indication of how favorable the mixed layer environment is for phytoplankton growth (Table 3). Critical depths were calculated to be 140, 185 and 285 m for February, March and April, respectively. These estimates were based on climatological averages of shortwave radiation at 38°N (BUNKER, 1976), and a measured extinction coefficient, k, of 0.058 (PHINNEY *et al.*, 1983). We also used the assumption that respiration, R, is 10% of the maximum photosynthesis rate, P_M, and the formula for critical depth given by LANGDON (1986).

$$D_{CR} = \frac{P_M/R\int_0^{DL}\sinh^{-1}(I_0(t)/I_K)\,dt}{k(24 - DL)} \quad (1)$$

$$I_0(t) = I_M \sin^3(\pi t/DL), \quad (2)$$

where $I_0(t)$ is the instantaneous irradiance, I_K is the light saturation coefficient, I_M is maximum irradiance, and DL is day length in hours. The value for I_K of 328 μE m^{-2} s^{-1} used for these calculations was derived from the photosynthetic performance–irradiance curves in LANGDON (1986). This formulation of critical depth differs from SVERDRUP (1953) in that photosynthesis saturates above irradiances above I_K. Failing to account for saturation will result in an overestimate of critical depth. For instance, LANGDON (1986) showed that the Sverdrup formulation for critical depth would overestimate D_{CR} by 11% with a total daily irradiance of 7.2 E m^{-2} d^{-1} and by 280% with a total daily irradiance of 59 E m^{-2} d^{-1}. This later irradiance value was close to the mean daily irradiance on clear days during our April cruise (Table 3). In April, critical depth was as great as 370 m on cloud-free days and as small as 170 m on overcast days. For comparison, YENTSCH and PHINNEY (1985), who used a different relationship from equation (1), reported a 440 m critical depth for WCR 82B in April.

The mixed layer depth was estimated to be close to 50 m at the time of ring formation in February (Fig. 11c, in SCHMITT and OLSON, 1985). Our observations show the mixed layer to be 300 m deep in March. The mixed layer deepened to 400 m by early April and was approximately 200 m deep (with large variation) in late April. Thus critical depth was deeper than mixed layer depth at the time of ring formation, shallower than mixed layer depth in March, and greater than average mixed layer depth by late April.

According to SVERDRUP (1953), this comparison suggests that the light environment was favorable to phytoplankton growth in February, unfavorable to phytoplankton growth in March, and again favorable in late April. In June critical depth was much greater than mixed layer depth, but in this case phytoplankton production was nutrient limited in the 10 m mixed layer.

Such classical interpretations of the relationship between mixed layer depth and critical depth assumes that the mixed layer is actively mixing at all times. As noted above, there may have been 11 times between February and early April when the deepening mixed layer was quiescent due to low winds or became temporarily stratified due to heat gain from the atmosphere. Such conditions would enhance phytoplankton growth by maintaining them in a favorable light environment for longer periods of time. This suggests that core waters of WCR 82B were more favorable for phytoplankton growth than implied by a simple comparison of mixed layer depth with critical depth.

Zooplankton biomass

Zooplankton are major consumers of primary produced carbon. The >333 μm zooplankton collected by the MOCNESS-1 are also sources and consumers of aggregate material found in the >53 μm MU(LVFS) samples. In March, zooplankton standing crop was relatively low and was uniformly distributed over the upper 1000 m (Fig. 8a). There was a significant increase in 0–1000 m zooplankton biomass by the time of April sampling, with a factor of two increase seen in the upper 200 m. By June, zooplankton biomass was strongly concentrated in the upper 50 m. These data indicate that stratifica-

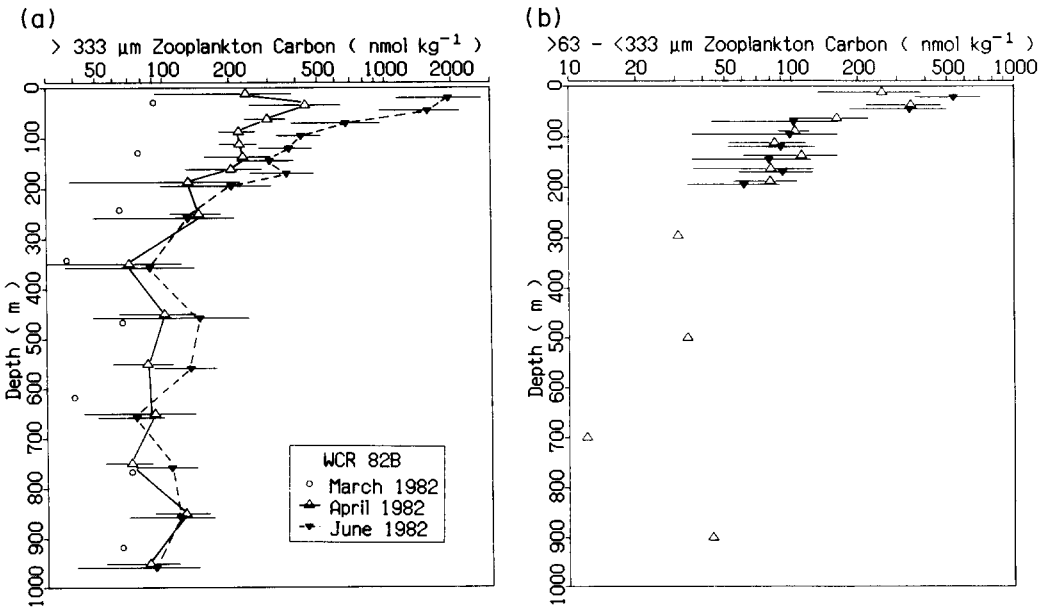

Fig. 8. (a) Distributions of >333 μm zooplankton carbon biomass in the upper 1000 m near the center of WCR 82B in March, April and June 1982. (b) >63 μm–<333 μm zooplankton carbon biomass in the upper 200 m in April and June 1982. The error bars shown in April and June data represent 1 S.D. of the zooplankton carbon biomass at the indicated depth. Only one MOCNESS tow was carried out in March.

tion of WCR 82B between April and June appeared to play a major role in determining the depth distributions of zooplankton.

To quantify the >333 μm zooplankton biomass changes between March and June (Fig. 9), the upper 400 m have been subdivided into 0–50 m and 50–400 m zones. The 50 m limit was chosen for the upper zone since all but a few percent of primary production occurred shallower than this depth in April. This 50 m layer also best represented the stratified portion of the water column (upper 40 m) in June within the 25 m resolution of the MOCNESS-1 tows. The 400 m limit was chosen since it represents the depth of greatest mixing over the February–June period.

Much of the zooplankton biomass gain in WCR 82B between March and June has been attributed to *in situ* growth (WIEBE *et al.*, 1985b). Mean biomass from 0 to 50 m at ring center increased from March levels of 92 to 340 nmol C kg^{-1} in April and to 1755 nmol C kg^{-1} by June, a factor of 3.7 gain between March and April and a further factor of 5.2 gain between April and June. This contrasts with the 50–400 m zooplankton biomass which rose from 64 nmol C kg^{-1} in March to 155 nmol C kg^{-1} in April and to 229 nmol C kg^{-1} in June, a factor of 2.4 increase between March and April but only an additional factor of 1.4 gain between April and June.

Specific analysis of zooplankton species biomass (DAVIS and WIEBE, 1985) showed that copepods contributed high percentages to the thermostad zooplankton biomass in March (44%) and April (57%) and low percentages (20%) in June. The three-fold increase in copepod biomass between March and April indicates that the growth herbiverous species was favored by conditions present in the thermostad over this time interval. This also suggests that WCR 82B was more productive over this period than indicated by comparison of mixed layer depth with critical depth. Copepod biomass in the 50–400 m interval dropped by a factor of two between April and June reflecting poorer growth

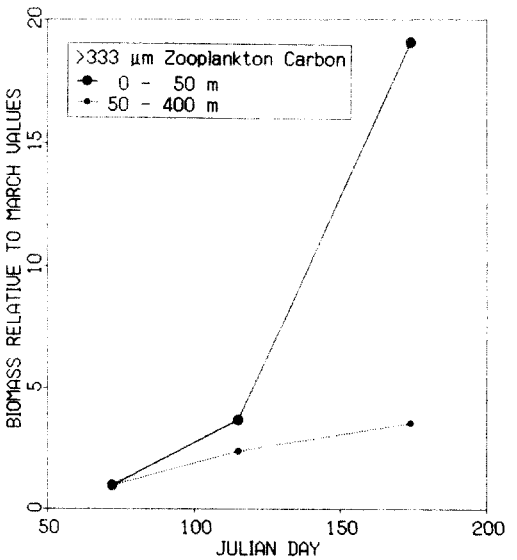

Fig. 9. >333 μm zooplankton carbon biomass changes in the 0–50 and 50–400 m depth intervals in core waters of WCR 82B normalized to biomass distributions determined in March 1982.

conditions and higher abundances of omnivorous and carnivorous zooplankton in the thermostad at that time.

MOC-1/4 data showed that the 64–333 μm zooplankton biomass was dominated by copepod nauplii and copepodite stages. The biomass of the 64–333 μm zooplankton in the 0–50 m interval increased by 40% from 300 to 430 nmol C kg^{-1} between April and June. Mean carbon biomass of same size fraction between 50 and 200 m decreased from 104 to 75 nmol C kg^{-1} between April and June. A single deep tow in April showed that 64–333 μm zooplankton biomass averaged 30 nmol C kg^{-1} between 200 and 400 m (Fig. 7B). Comparisons with MOCNESS-1 data show that the thermostad biomass was dominated by >333 μm zooplankton in both April and June.

Zooplankton grazing

In situ grazing estimates in April averaged 3% (range 1–5%) of daily primary production to 50 m but averaged 16% (range 10–40%) of primary production to 25 m in June. As mentioned above, all but a few percent of primary production occurred shallower than these depths during April and June. Grazing by large calanoid copepod species, not readily captured in the *in situ* feeding chambers but sampled by the MOC-1, averaged 44% of daily primary production in April and 125% of mean primary production in June (Cowles and Copley, personal communication). Summing these two types of grazing estimates, it was found that >64 μm zooplankton grazed approximately 50% of primary production in April and 140% of primary production in June. The fact that >100% of primary production was estimated to be consumed by zooplankton is taken as an indication of the magnitude of error in grazing estimates. The relatively constant levels of phytoplankton biomass and primary production during the June cruise (Hitchcock *et al.*, 1985) also suggest that phytoplankton production and consumption were in balance in WCR 82B in June.

Particulate matter

Although our earliest particulate matter data were collected in April, it is a useful exercise to estimate what average particle concentrations may have been in the upper 400 m in February at the time of ring formation. To do this we have used MU(LVFS) data from the Gulf Stream and Sargasso Sea in August 1982 and from WCR 82H in October 1982. WCR 82H was in the process of formation at the time of sampling and thus had particle distributions typical of the Gulf Stream–Sargasso Sea transitional waters from which the ring formed. LVFS samples collected from the warm side of a Gulf Stream meander in mid-October 1974 (R.V. *Atlantis* II 85; Bishop, unpublished data) were not significantly different from samples collected from the Gulf Stream, Sargasso Sea, and WCR 82H in 1982.

We are justified in using suspended particulate matter (SPM) data from the stratified waters of the Gulf Stream, Sargasso Sea and WCR 82H to describe distributions probably present in WCR 82B in February for the following reasons. The first argument for stratification of WCR 82B at the time of its formation comes from the fact that the waters which formed the ring are part of the flow regime of the Gulf Stream (Halkin and Rossby, 1985) and thus were derived from lower latitudes where the water column is permanently stratified. A second argument is that models of the thermal evolution of WCR 82B which best match the temporal development of mixed layer depth as observed in March and April suggest that a mixed layer 50 m deep was present at the time of ring

formation (SCHMITT and OLSON, 1985). Data from the Sargasso Sea near Bermuda also show that mixing significantly deeper than 100 m occurred only two or three times in 20 years (MENZEL and RYTHER, 1961; JENKINS and GOLDMAN, 1985). The lack of deep mixing events in the Sargasso Sea is also consistent with MENZEL and RYTHER (1970) who found little evidence of variability of particulate carbon below 100 m.

More recent observations of particulate carbon in the Sargasso Sea (GORDON, 1977, GORDON *et al.*, 1979) established that particulate carbon concentrations below 100 m were temporally variable, but also showed that the magnitude of variability was small. Excluding Gordon's single observation during a spring bloom in late March 1972, particulate carbon variability (range/mean; $n = 8$) was 58% in the 0–100 m depth interval. The 100–1000 m interval showed higher variability (128%). If we exclude Gordon's earliest observation from October 1971, then 100–1000 m variability dropped to <43%. Since Gordon's October 1971 data are inconsistent with LVFS data from 2 years in the same month, they may have been collected in a cold-core ring. The final rationale for our extrapolation is to provide a context for explaining the April and June particle distributions. In other words, the SPM variability that will be described below significantly exceeds that found by Gordon.

The *probable* SPM concentrations typical of the upper 400 m in February at the time of ring formation were estimated as follows. First, all data from the Gulf Stream, Sargasso Sea and WCR 82H were binned into 50 m depth intervals. Average concentration was then calculated for each bin. We then averaged the 50 m bin data from 0 to 700 m. The 700 m limit corresponded to the depth of the 15°C isotherm and most closely matched the 0–400 m water column believed to be present at the time of ring formation in February 1982. April averages were calculated using any LVFS cast within 30 km of ring center and June averages combined data from both LVFS and MULVFS casts within 30 km of ring center (Table 2). Thermostad averages for April and June were calculated for the 0–400 and 40–400 m intervals, respectively.

There were almost uniform and relatively high particulate matter concentrations in the thermostad of WCR 82B during 22–23 April (Fig. 10). For example, the 45 μg kg^{-1} particle concentration found at 325 m was 4–5 times greater than particle concentrations found in stratified waters between 100 and 400 m in the Gulf Stream, Sargasso Sea or in the newly formed WCR 82H. Since lateral transport processes were relatively unimportant in WCR 82B, the high concentration in the deep mixed layer were clearly related to the fact that convective overturning of the water column was in progress or had occurred close to the time of sampling.

One profile collected between 0 and 200 m on 28 April (JD 118) before the storm on 29 April showed evidence for growth of phytoplankton at the surface and consumption of particles in the deeper waters. The chlorophyll cast immediately following the LVFS profile (JD 118, Fig. 5) also indicated water column quiescence. The advent of the storm and subsequent mixing resulted in mixed layer convection over at least the upper 200 m as indicated by the chlorophyll data on 30 April. Deep mixing of surface derived particulate matter due to the 29 April storm was also indicated on 1 May where replicate samples from 310 m again showed relatively high SPM levels.

June data showed SPM concentrations up to 400 μg kg^{-1} in the pycnocline between 20 and 50 m. Concentrations rapidly dropped to <25 μg kg^{-1} by 100 m and to <15 μg kg^{-1} by 400 m. The absence of down mixing events when the ring was stratified confined

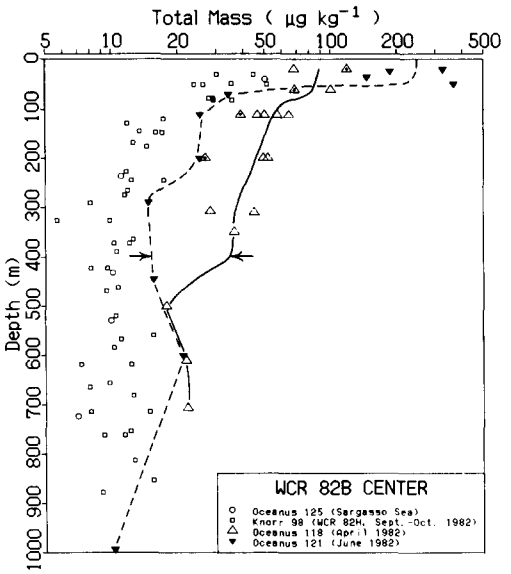

Fig. 10. Distributions of total >1 µm particulate dry weight in the upper 1000 m of WCR 82B. Data from WCR 82H and from the Sargasso Sea are shown to indicate probable distributions of particulate matter at the time of ring formation in February. The solid and dashed lines denote the trends of the April and June data, respectively. The base of the thermostad was at 400 m in April and June and is indicated by horizontal arrows. Multiple data points at a single depth are analyses of independently collected particulate matter samples. Error in analysis is smaller than the size of a single symbol. The data show significant changes in particle distribution over the upper 1000 m between probable February values and those determined in April and June 1982. Triangles filled with small circles denote samples collected on 28 April when the water column was transiently stratified or quiescent.

phytoplankton within the euphotic zone and reduced the rate of supply of surface produced particulate matter to the deep thermostad. Thus the state of stratification of WCR 82B in April and June had a profound effect on particle distributions.

Mean thermostad SPM concentrations

When compared with assumed source waters (assuming Sargasso Sea and WCR 82H data as a reference for February distributions), the total particulate matter dry weight averaged over the upper 400 m increased from probable February levels of 15 µg kg^{-1} to 55 µg kg^{-1} in April. Levels decreased in the 40–400 m thermostad to 22 µg kg^{-1} by June.

Particulate carbon, phosphorus, calcium and silicon in the thermostad exhibited similar temporal trends as found for dry weight (Figs 11–14). The second order trend behavior of calcium carbonate and silica contrasted with the organic constituents in that calcium showed a less pronounced gain but a stronger relative loss and silica showed no significant loss at all in June. This is attributed to the relative shift of primary production strongly in the favor of silica precipitating organisms over calcareous organisms. Such a shift is confirmed by changes in bulk Si:Ca mole ratio from a probable 1.3:1 in February to 2.0:1 in April to 6.1:1 in June.

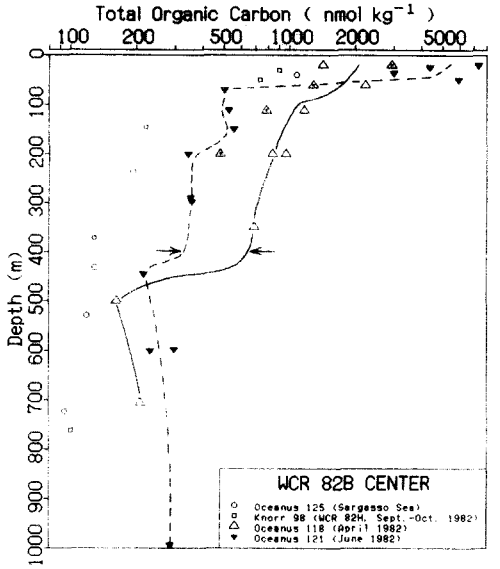

Fig. 11. Distributions of >1 μm particulate organic carbon in the upper 1000 m of WCR 82B. Probable distributions are shown for February based on WCR 82H and Sargasso Sea data. The solid and dashed lines indicate the trends of April and June data, respectively.

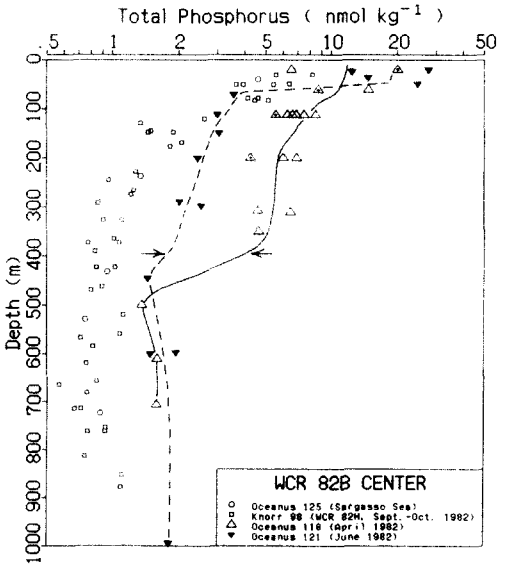

Fig. 12. Distributions of >1 μm particulate phosphorus in the upper 1000 m of WCR 82B. The data again show the substantial increase in particulate phosphorus loading in the thermostad between February and April and the significant removal of particulate phosphorus from the thermostad between April and June 1982.

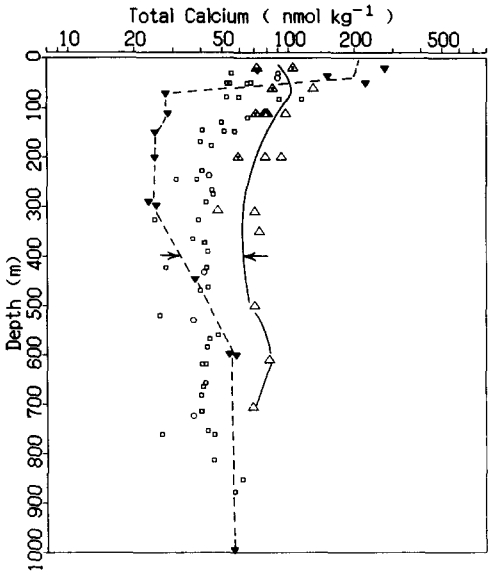

Fig. 13. Distributions of >1 μm particulate calcium in the upper 1000 m of WCR 82B. Although the first order trends are the same as for dry weight and organic components, calcium exhibited a lower relative increase between February and April and a greater relative removal between April and June.

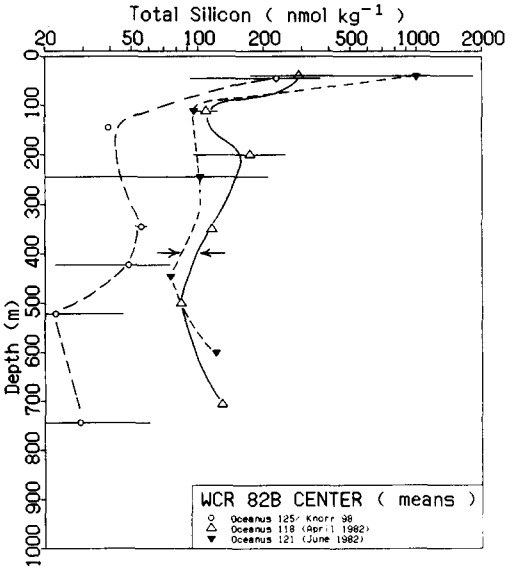

Fig. 14. Distributions of >1 μm particulate silica in the upper 1000 m of WCR 82B. Shown are the means and standard deviations of data from the sample analyses for probable February conditions, April and June profiles. Particulate silica showed a relative increase between February and April but did not show any significant drop in thermostad concentrations between April and June. The relative changes of particulate calcium (Fig. 13) and silica in thermostad waters reflect the fact that siliceous phytoplankton increasingly dominated production relative to calcareous phytoplankton from February to June.

Accumulation of loss of SPM in the thermostad

All particulate components were converted to integrated 0–400 m standing stocks and the net gain and loss of particulate matter was calculated for the intervals between February and April and between April and June (Table 4). The choice of a 400 m as opposed to a 360 m interval of integration for June, was made to provide a uniform basis for comparison of data over the three time periods.

Integrated dry weight increased from 6 g m^{-2} in February, to 22 g m^{-2} in April and decreased to 9 g m^{-2} in June. Net particle fluxes to and from the thermostad were calculated by dividing these numbers by 60 days (Table 5). Results show an average gain of 270 mg m^{-2} d^{-1} over the period February–April and a subsequent loss of 223 mg m^{-2} d^{-1} between April and June. These gains and losses are the same magnitude as vertical mass fluxes reported for the Slope Water (GARDNER, 1977; ROWE and GARDNER, 1978) and are 5–6 times higher than mass fluxes reported for the Sargasso Sea off Bermuda (DEUSER and ROSS, 1980).

Organic carbon fluxes calculated in a similar fashion showed a 5.5 mmol m^{-2} d^{-1} gain between February and April and a 4.6 mmol m^{-2} d^{-1} loss between April and June. These fluxes amounted to a storage of approximately 10% of carbon fixed by phytoplankton between February and April and a utilization of an additional 6% in excess of primary produced carbon between April and June. Phosphorus fluxes followed those of organic carbon and showed a 40 μmol m^{-2} d^{-1} gain and 35 μmol m^{-2} d^{-1} loss. C:P flux ratios were 140:1 and 130:1 for uptake and loss, respectively. This flux ratio was 30% higher

Table 4. Thermostad particle budgets

Quantity	Mean thermostad concentrations February*	April	June
Dry weight (μg kg^{-1})	14.7	54.9	21.5
Organic carbon (nmol kg^{-1})	257	1088	392
Inorganic carbon (nmol kg^{-1})	46	80	26
Biogenic silica (nmol kg^{-1})	60	164	161
Phosphorus (nmol kg^{-1})	1.65	7.6	2.3
Integrated values†			
Dry weight (g m^{-2})	5.88	21.96	8.6
Organic carbon (mmol m^{-2})	102.8	435.2	156.8
Inorganic carbon (mmol m^{-2})	18.4	32	10.4
Biogenic silica (mmol m^{-2})	24	65.6	64.4
Phosphorous (mmol m^{-2})	0.66	3.04	0.92

* Based on data from the Sargasso Sea, Gulf Stream, and WCR 82H.

† Assuming a 400 m thick layer.

*Table 5. Net thermostad particle fluxes**

Quantity	February–April	April–June
Dry weight (mg m^{-2} d^{-1})	268	−223
Organic carbon (mmol m^{-2} d^{-1})	5.54	−4.64
Inorganic carbon (μmol m^{-2} d^{-1})	227	−360
Biogenic silica (μmol m^{-2} d^{-1})	693	−20
Phosphorous (μmol m^{-2} d^{-1})	39.7	−35.3

* Assuming a 60 day period between cruises.

than the C:P ratio of organic matter inferred from nutrient distributions in the main thermocline (TAKAHASHI *et al.*, 1985).

Carbonate carbon accumulation (227 μmol m^{-2} d^{-1}) was 4% of organic carbon accumulation, and carbonate loss (360 μmol m^{-2} d^{-1}) was 7.8% of organic carbon loss over the same time periods. The accumulation of biogenic silicon was 690 μmol m^{-2} d^{-1} between February and April and no significant loss between April and June was observed.

The fact that total particulate mass, organic carbon, phosphorus, silicon and calcium distributions exhibited such substantial temporal variability also underscores the fast turnover times possible for small, slowly sinking particles in productive water columns.

Large aggregate particles

The profiles of the abundances of both fecal matter and fecal pellets can be used to indicate the feeding activities of zooplankton in the water column. This is because both fecal matter and fecal pellets are produced by zooplankton which feed on phytoplankton carbon produced in the euphotic zone and fecal material is consumed by coprophagous zooplankton resident in the deeper water column.

The larger than 1 mm sized fecal matter and fecal pellets have been shown to have settling residence times in the upper 1000 m of <10 days (FOWLER and SMALL, 1972; BISHOP *et al.*, 1978). Therefore their abundances in the water column are closely linked to the environmental conditions present at the time of sampling. The size distributions of fecal matter in the water column are sufficiently well behaved that concentrations of this material are closely related to vertical particle flux carried by this class (BISHOP *et al.*, 1980).

Fecal matter

Fecal matter (BISHOP *et al.*, 1977) is an important contributor to sedimentation and is a subset of amorphous macroscopic aggregates which are collectively described as "marine snow" by SILVER *et al.* (1978) and ALLDREDGE and COX (1982). Fecal matter ranges from 50 μm to cm in size, has little symmetry, but contains many of the same kinds of small particles as found in fecal pellets. The name fecal matter is kept for consistency with previous publications, although the source organisms for this material and the mechanisms of its formation still remain a mystery.

In late April, thermostad >1 mm fecal matter concentrations (by number) ranged from 10 to 20 m^{-3} (Fig. 15), a substantial increase over probable February values of <1 m^{-3}. Fecal matter counts on two samples from 20 and 60 m on 28 April could not be made from the contact prints due to heavy loading of the 53 μm Nitex with smaller particles. By 1 May a 6-fold increase in fecal matter concentration to 70 m^{-3} at 310 m was noted. This high value was replicated to within several percent by a test deployment of the prototype MULVFS filtration unit at the same depth several hours later. Simultaneously, fecal matter abundances at 600 m increased from 1.5 to 10 m^{-3}, suggesting an overall increase in vertical particulate matter flux between 23 April and 1 May.

By June, a 10–20 fold increase to nearly 200 m^{-3} in >1 mm fecal matter abundance was observed in near-surface waters, consistent with the strong accumulation of zooplankton biomass in the surface waters. Also consistent with the strong increase in near-surface zooplankton biomass was the nearly 100-fold drop in concentration between the fecal matter maximum at 40 and 110 m (Fig. 14). Such a strong concentration gradient

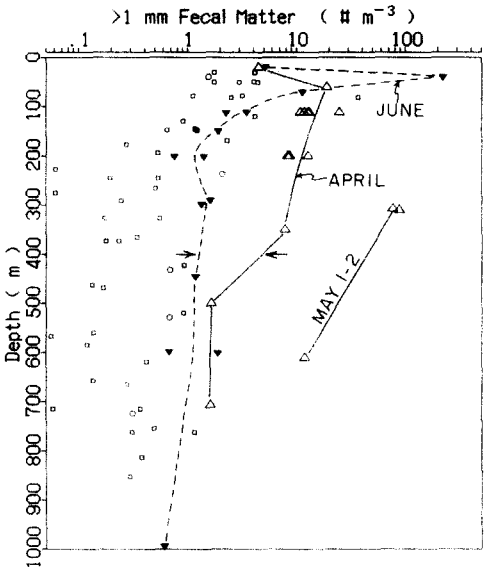

Fig. 15. Distributions of >1 mm sized fecal matter in the upper 1000 m of WCR 82B. The data show an order-of-magnitude increase in the abundance of this aggregate material between probable February levels and April. A further 6-fold increase in the abundance of fecal matter was observed at 300 and 600 m in early May. By June, a further 10-fold increase in the abundance of this material were observed at 40 m relative to April levels, consistent with the increased zooplankton biomass. Fecal matter abundances dropped 100-fold by 110 m indicating that intensive particle recycling was occurring in the shallower waters.

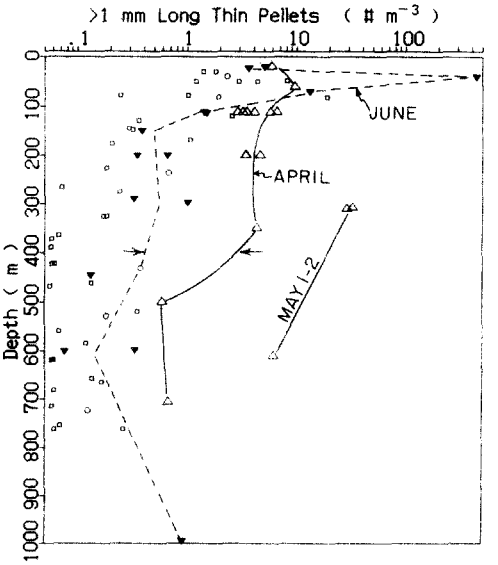

Fig. 16. Distributions of >1 mm long fecal pellets in the upper 1000 m of WCR 82B. The data show the same temporal trends as found for fecal matter indicating that the processes governing the production and destruction of these particles in the water column operate in concurrent fashion.

has never been observed before in LVFS profiles and appears to reflect the highly efficient grazing conditions found in June.

Abundances of long, thin fecal pellets exhibited the same temporal trend as did fecal matter (compare Figs 15 and 16). It appears that the factors governing the production and destruction of these two classes of particles operate in a concurrent fashion. Since the >1 mm long fecal pellets are known to be produced by zooplankton (e.g. FOWLER and SMALL, 1972; KOMAR *et al.*, 1981) and since fecal matter abundances strongly covary with fecal pellets, it is likely that these particles are all the result of macrozooplankton and micronekton feeding activities. Furthermore, the presence of strong >1 mm particle gradients in June (as compared to weak gradients in April) is consistent with the indication of greatly increased zooplankton grazing pressure in the upper 50 m in June.

DISCUSSION

We have presented data on the physics, hydrography, primary productivity, zooplankton distributions, zooplankton grazing activity, and particle field within the semi-isolated core waters of WCR 82B from February to June 1982. These data show a coherent picture of the influence of the physical environment on biological processes governing the production and distributions of particulate matter. Particulate matter accumulated in the thermostad as a result of continued mixing events between the time of ring formation in February and late April and particulate matter was lost from thermostad waters after seasonal stratification of the water column in early May. The distributions of zooplankton and euphotic zone measurements of zooplankton grazing rates suggest in April that the zone of particle utilization (by zooplankton) was spread over a depth range of several hundred meters in the thermostad. By June, the zone of particulate matter utilization was sharply confined to the upper 50 m of the water column. The major processes and reactions of the various components of the particle production and utilization system and how they may have operated to produce the conditions observed in April and June can now be described semi-quantitatively (Fig. 17).

In April, zooplankton grazing in the upper 50 m consumed approximately 50% of the daily 92 mmol C m^{-2} d^{-1} phytoplankton growth. This 46 mmol C m^{-2} d^{-1} rate is probably an upper estimate since the upper 50 m contained approximately 23% of the >333 μm zooplankton biomass present in the 400 m deep thermostad, and the composition of the zooplankton was not appreciably different over this interval (DAVIS and WIEBE, 1985). At depths shallower than 50 m, phytoplankton biomass did not accumulate in April (Fig. 6) and no other biological removal process could be identified. It is therefore concluded that mixing below the euphotic zone was the other major removal process for PP in April. This conclusion is also supported by the chlorophyll, nutrient and XBT data presented above.

We can estimate how much primary produced material was mixed below the euphotic zone between February and April as follows: It was shown above that PP was probably 29 mmol C m^{-2} at the time of ring formation in February, and that PP probably was near 48 mmol C m^{-2} d^{-1} in mid-March. April levels were measured to be 92 mmol C m^{-2} d^{-1}. If a linear increase of production between February and March and between March and April is assumed, then average production for the February–April period was 57 mmol C m^{-2} d^{-1}.

As noted above, >64 μm zooplankton grazing estimates show that 50% of primary

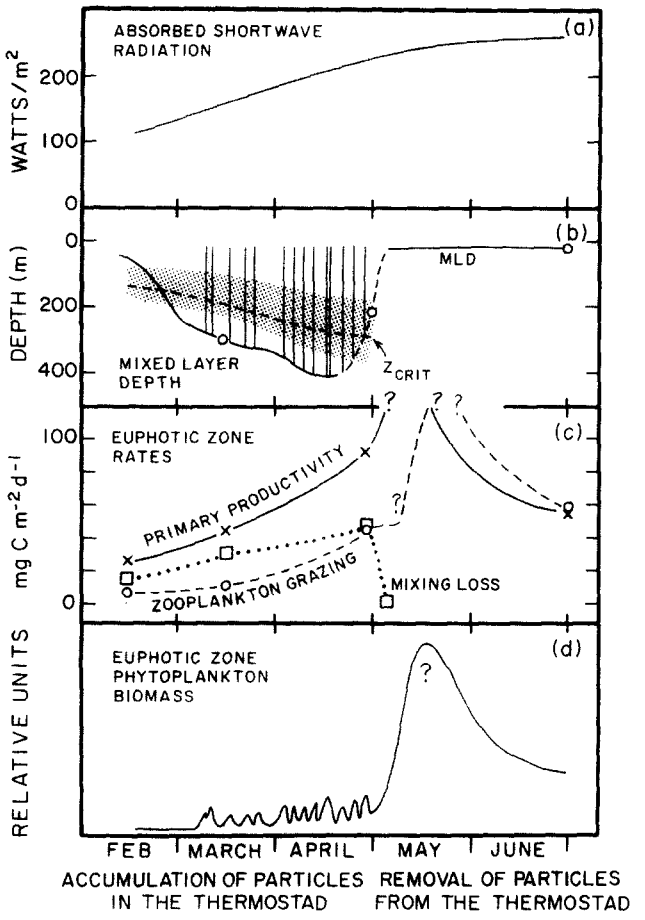

Fig. 17. A schematic representation of processes affecting particulate matter in the euphotic zone of WCR 82B from the time of ring formation in February to June 1982. (a) Absorbed shortwave radiation (average over a 24 h period) from BUNKER (1976). (b) Temporal trends of thermostad depth (redrawn from SCHMITT and OLSON, 1985). The vertical lines are drawn at times when heat budget calculations showed the ring to be gaining heat. At these times transient stratification and quiescence of core waters may have occurred. Also shown are trends for critical depth. Dashed line is based on LANGDON (1986, submitted) and climatological averages of absorbed shortwave radiation. The stippled area corresponds to the range in critical depth due to variations in cloudiness. (c) The temporal trends of euphotic zone primary productivity (mmol C m^{-2} d^{-1}), zooplankton grazing, and of down mixing of primary produced carbon. (d) Schematic trend of euphotic zone phytoplankton biomass. The small spikes shown prior to stratification are drawn to indicate phytoplankton growth during periods of transient stratification of quiescence. Question marks indicate uncertainty about the shapes of the curves between early May and June.

production was utilized by zooplankton in April (with <5% being accounted for by <333 μm animals), and it was concluded that the other 50% loss of PP from the euphotic zone was due to down mixing. If we assume that grazing in the upper 50 m is proportional to >333 μm zooplankton biomass, then a carbon specific rate of 2.7 mmol C d^{-1} per mmol of zooplankton carbon is calculated. If we apply this to the March profile, zooplankton grazing rates are estimated to be 12.4 mmol C m^{-2} d^{-1}, or

26% of primary production. If a similar percentage applies to February as well, then zooplankton grazing is estimated to be 8 mmol C m^{-2} d^{-1}. Linear interpolation of these data suggests that 19 mmol C m^{-2} d^{-1} (or roughly 33% of primary production) was consumed by zooplankton in the upper 50 m between February and April. Therefore, mixing yields a mean supply rate of carbon of 38 mmol C m^{-2} d^{-1} (or 67% of primary production) to thermostad waters deeper than 50 m. Over a period of 60 days, this supply rate would contribute to an increase of 6510 nmol C kg^{-1} in a 350 m thick layer.

The mean thermostad particulate carbon concentration was observed to have increased by 830 nmol C kg^{-1} between February and April, approximately 13% of particulate carbon delivery by mixing. This translates into an average increase in standing stock of 290 mmol C m^{-2} in the thermostad between 50 and 400 m. With a supply rate of 38 mmol C m^{-2} d^{-1} this increase in standing stock would have been possible in only 8 days time. Similarly, with a particulate carbon concentration of 1088 nmol kg^{-1}, it would be possible to replace all particulate carbon in the 50–400 m water column in 10 days. Such calculations suggest that rates of particle supply (by mixing and settling from above) and removal (consumption, respiration and settling) were close to being in balance. Also this result shows that particle populations in productive, deep mixed layers can turn over on the time scale of days.

The meteorological evidence presented suggests that the last major mixing event which supplied significant amounts of material to the thermostad occurred on 29 April and that seasonal stratification was established in early May. The consequence of this sequence of events was that the down-mixed supply of primary produced carbon to the thermostad was strongly reduced over a period of several days. During April, the supply of particulate carbon by mixing was 46 mmol C m^{-2} d^{-1}. If this supply rate was balanced by the removal rate, then the standing stock of SPM in the 50–400 m water column could be depleted in as short a period as 6 days following the establishment of seasonal stratification in May and the cessation of SPM delivery by mixing. Removal rates on such short time scales are consistent with the variability in SPM and chlorophyll data. The April–June differences in standing stocks of particulate carbon in the thermostad below 50 m yields an average removal rate of 4.1 mmol C m^{-2} d^{-1}. Hence the particle removal rates must have declined rapidly following the onset of seasonal stratification.

The loss of the down-mixing sink for primary produced carbon in the upper 50 m at the onset of stratification has a second consequence: primary production rates in this layer exceeded known rates of removal by a factor of two. With a C:N ratio of 7.0 and with the 92 mmol C m^{-2} d^{-1} PP as measured in April, the 5.6 μmol NO_3^- kg^{-1} would be stripped from the upper 25 m in 11 days time. With a grazing loss of 50%, 490 mmol m^{-2} of particulate carbon would accumulate in the same depth interval over this time, resulting in a concentration of 19,600 nmol C kg^{-1}, roughly 3 times the highest levels observed in June (Fig. 11).

In apparent response to the loss of food supply upon stratification, the herbivorous zooplankton within the thermostad would shoal towards the food source at the surface (Fig. 8). The progressive increase of zooplankton biomass in the euphotic zone due to growth and upward migration from below would increase grazing pressure until once again production and utilization were in balance. Such a balance is believed to have been sampled in June. The data on the vertical distributions of zooplankton and large aggregate abundances at this time suggest that particulate matter was being rapidly recycled within the upper 100 m.

The temporal trends of primary production in the Sargasso Sea near Bermuda described by MENZEL and RYTHER (1960, 1961) are entirely consistent with our description of the coupling between primary production, physical processes and zooplankton. Differences between WCR 82B and the Sargasso Sea near Bermuda are: (1) prior to stratification, nutrient levels in the deep mixed layer of WCR 82B were at least 3 times higher than the highest values reported by MENZEL and RYTHER (1960), and (2) after stratification, WCR 82B continued to have high nutrient fluxes into the euphotic zone as a result of upwelling of thermostad waters induced by frictional decay of the ring (FRANKS *et al.*, 1985, NELSON *et al.*, submitted). In the Sargasso Sea, the absence of upwelling resulted in a rapid depletion of nutrients and a rapid decline in primary production. The dynamics of WCR 82B is also consistent with observations made by SVERDRUP (1953) who found that mixing in deep mixed layers maintained low levels of phytoplankton biomass and that after stratification a phytoplankton bloom occurred. Later on, zooplankton determined the fate of the bloom. We differ from Sverdrup in the fate of the carbon below the euphotic zone in a deep mixed layer. Our data suggest that zooplankton grazing in the deep mixed layer, instead of phytoplankton dark respiration, is the dominant mode of particle removal. We also suggest that it is the imbalance between production and removal in the euphotic zone coincident with stratification that leads to the development of the phytoplankton bloom.

CONCLUSIONS

In warm-core ring 82B, particulate matter distribution was a sensitive indicator of the dynamics of the carbon cycle and particularly of the balance between production and grazing demand. Particle concentrations increased in the convectively deepening mixed layer between February and April. During this time approximately 67% of primary produced carbon was mixed below the euphotic zone into the thermostad. Such a down-mixing supply was favorable for the growth of herbivorous zooplankton which were found to be distributed nearly uniformly between 50 and 400 m. The analysis presented here suggests that the particles in the thermostad turned over on time scales of approximately 10 days. After the onset of stratification in early May 1982, the convective down mixing of PP was eliminated, and particle production and removal were no longer in balance. This must have resulted in a phytoplankton bloom, the development of which was evident in CZCS images from 1 to 7 May, and which probably peaked in the middle of May. Calculations suggest that particulate matter was lost from thermostad waters below the euphotic zone following seasonal stratification and that this loss may have occurred over as short a time as 1 week. Following the removal of deep particulate material, the zooplankton biomass shoaled to become concentrated in the upper 100 m of the water column. The continued high primary production of WCR 82B and increased zooplankton biomass in the upper 50 m in June resulted in the production of large quantities of aggregate particles in the upper 40 m and the strong removal of this material by 110 m.

The results presented from the study of WCR 82B demonstrate that physical processes closely determine the vertical distributions of phytoplankton, zooplankton and particulate matter, i.e. the biological state of the water column. It is hypothesized that the coupling of primary production, mixing and zooplankton grazing operates in other warm-core rings of the Gulf Stream, Kuroshio and East Australian Current which experience

the formation of thermostad layers in the winter season. Furthermore, the process coupling described above is probably applicable to wider oceanic regions where deep mixed layers are formed.

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